Nutrient cycles in pine and their adaptation to poor soils

HUGH G. MILLER, JEAN M. COOPER, JOHN D. MILLER, AND OLIVE J. L. PAULINE

The Macaulay Institute for Soil Research, Craigiebuckler, Aberdeen, AB9 2QJ Scotland

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Values for the various fluxes of nitrogen through the tree–soil system were calculated using models derived from measurements of rates of input, accumulation, and transfer in plots of 11-m-tall *Pinus nigra* var. *maritima* (Ait.) Melv. that were showing growth responses to varying rates of nitrogen fertilizer. As the result of continuing immobilization in trees and humus, growth of the unfertilized trees was declining and the trees were having to sacrifice older tissues to mobilize sufficient nitrogen for new growth. In the fertilized trees, there was similar mobilization but of excess nitrogen stored during the period that fertilizers were applied. Models of the flux of nitrogen, phosphorus, calcium, and magnesium at optimum growth showed that tight cycling and low rates of immobilization, coupled with effective retention of relatively high atmospheric inputs, probably represents the adaptive mechanism that enables trees to thrive on soils low in potassium and magnesium. However, high rates of immobilization and low rates of atmospheric input relative to tree uptake mean that despite the maintenance of tight cycles, the trees continued to make significant demands on soil reserves of nitrogen, phosphorus, and calcium throughout their life cycle.

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Les auteurs ont calculé les divers flux d'azote circulant dans le système sol:arbre en utilisant des modèles dérivés de mesures des taux d'intrants, d'accumulation et de transfert de cet élément dans des parcelles de *Pinus nigra* var. *maritima* (Ait.) Melv. de 11 m de hauteur; la croissance de ces pins répondait à l'application d'engrais azoté. Comme résultat de l'immobilisation continuelle dans les arbres et l'humus, la croissance des arbres non fertilisés montrait un ralentissement, accompagné du dépérissement des vieux tissus, consécutif à une mobilisation de l'azote pour la croissance nouvelle. Chez les arbres fertilisés, il s'est produit une mobilisation de l'excès d'azote emmagasiné au cours de la période suivant l'application d'engrais. Les modèles de flux d'azote, de phosphore, de calcium et de magnésium, au moment de la croissance optimum, révèlent qu'un cyclage fermé, un taux élevé d'immobilisation, et une rétention efficace des apports atmosphériques constituent probablement le mécanisme d'adaptation permettant aux arbres de se développer sur sols pauvres en potassium et en magnésium. Toutefois, les taux élevés d'immobilisation et les faibles taux d'apports atmosphériques en regard du prélèvement par les arbres, indiquent que malgré le maintien de cycles fermés, les arbres continuent à entamer d'une façon significative les réserves en azote, en phosphore et en calcium du sol, tout au long de leur cycle vital.

[Traduit par le journal]

Introduction

A feature of many tree species, in particular the pines, is that they are well adapted to young soils typically low in both organic matter and exchangeable nutrients. These species, therefore, must have evolved special mechanisms to cope with nutritionally poor sites. Essentially five possible components of such mechanisms can be suggested. The first, that trees need less of any nutrient than do other plants, can be regarded as insufficient explanation in light of recent measurements of nutrient uptake (e.g., Duvigneaud and Denaeyer-De Smet 1970; Ulrich and Mayer 1972; Johnson and Risser 1974; Mälkönen 1974; Miller, Miller, and Pauline 1976; Likens *et al.* 1977). The remaining four possibilities are (*i*) the conservation of available nutrients by maintaining "tight" nutrient cycles (Bormann *et al.* 1977) from which losses to deeper soil layers or to the atmosphere are very small, (*ii*) the minimizing of temporary losses from the cycle through immobilization, particularly in the soil organic layers, (*iii*) the collection, and retention within the cycle, of nutrients from the atmosphere such as those in rain and aerosols, and (*iv*) the evolution of special means

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of obtaining nutrients from intractable soil sources. Irrespective of which and how many of these apply to a particular nutrient and species, the ecosystem must in extreme cases be very sensitive to any disturbance that might reduce the ability to obtain, retain, or cycle nutrients. As such disturbances can include pollution (Tamm 1976) and management practices, including harvesting methods (Likens *et al.* 1978), use of fertilizers (Fagerström and Lohm 1977), and prescribed burning (Sirén 1973; Kimmins and Feller 1976), there is a need to obtain a clear understanding of the interrelated processes involved.

Recently, an integrated study has been made of the cycle of nutrients, their relationship to growth, and the changes following addition of fertilizer in a 36-year-old crop of Corsican pine (*Pinus nigra* var. *maritima* (Ait.) Melv.) planted on bare sand dunes. The results were used to derive models to predict the values of nutrient flux between zones of accumulation (Miller, Miller, and Pauline 1976). In this paper, these predictions are discussed in the context of the complete cycles of major nutrients and the maintenance of these cycles on sites of low fertility.

Experimental Site

Culbin sands is an area of aeolian coastal dunes on the southern shore of the Moray Firth in northeast Scotland (57°32′N latitude, 3°43′W longitude). This area is in the northern temperate subzone of Scotland (Birse 1971), having warm summers (accumulated day degrees > 1375°C) and fairly mild winters, although it is somewhat exposed, particularly to the sea which lies to the north and northeast. Annual rainfall is only 630 mm. Moisture stress, generally, in late summer, can affect tree growth, but during winter and spring, the water table level is quite high. The forest is planted mainly with pine species, and although these show varying degrees of nitrogen deficiency (Miller and MacKenzie 1965), fertilizer trials suggest that other elements are in adequate supply.

When planted in 1928, the dunes, which previously had been fairly mobile, carried only sparse vegetation and there was no soil organic layer. By 1964, the crop contained 2110 stems ha^{-1} and had reached a mean height of 11 m, a basal area of 36.6 $m^2\ ha^{-1}$, and a volume of 209 $m^3\ ha^{-1}$ (an estimated 43 $m^3\ ha^{-1}$ having previously been removed in two light thinnings). Within this stand, a fertilizer experiment was laid out consisting of three replicates of five treatments in randomized blocks. All plots were given a single light dressing of 21 kg ha^{-1} phosphorus and 120 kg ha^{-1} potassium. The experimental treatments were 0, 84, 168, 336, and 504 kg $ha^{-1}\ year^{-1}$ nitrogen, applied as ammonium sulphate and repeated each year for 3 years (Miller and Cooper 1973).

The unfertilized control trees were very nitrogen deficient, a deficiency that was becoming more pronounced with time, and growth responded strongly to the fertilizer application. Thus, whereas the control trees grew only 10.4 $m^2\ ha^{-1}$ over the 14 years from 1964 to 1977, the treated trees grew 12.8, 16.0, 17.7, and 19.8 $m^2\ ha^{-1}$ with increasing treatment rate, a linear response that is significant ($P < 0.01$). By 1977, responses to the two lower rates had ceased, but the two upper rates were still stimulating significant ($P < 0.05$) growth responses of 44% and 75%, respectively.

Methods

Whole trees (including roots) were sampled from across the size range in each treatment prior to the fertilizers being applied and again after the 3-year period of treatment (Miller, Miller, and Pauline 1976). Samples were also collected of the soil and forest floor. Litter fall was sampled over 6 years starting at the outset of the experiment, and during the middle 2 years, the movement of nutrients in rainwater was monitored in three of the five treatments (Miller, Cooper, and Miller 1976).

All vegetation samples were dried at 70°C, subsampled, ashed at 500°C, and dissolved in hydrochloric acid. Potassium and calcium were determined by flame emission spectrometry, and magnesium was determined by porous-cup spark emission (Mitchell 1964) or by atomic absorption spectrometry. Phosphorus in vegetation was measured by the vanadomolybdate method (Kitson and Mellon 1944), and that in water was measured using the Truog and Meyer reagent and stannous chloride. Nitrogen in rainwater was determined as ammonium and nitrate, and organic nitrogen was determined by methods similar to those of Carlisle *et al.* (1966). For samples of vegetation and soil, total nitrogen was determined by a semi-micro-Kjeldahl method.

From these results, regressions were derived both relating weights of tree components to crop basal area and age and relating percentage nitrogen in these components to the concentration in top-whorl foliage. As the relationship between percentage nitrogen in top-whorl foliage and growth had been established for this crop (Miller and Cooper 1973), it was then possible to calculate the amount of nitrogen accumulated by the trees at different growth rates. Release of nitrogen in litter fall was derived from regressions on growth rate and release through crown leaching obtained from the measured relationship with concentration in top-whorl foliage. These regressions were then combined to calculate the nitrogen flux associated with particular growth rates for an approximately 40-year-old crop of Corsican pine (for details see Miller, Miller, and Pauline 1976). Similar calculations were made for phosphorus, potassium, calcium, and magnesium using concentration levels for living tree components recorded at the end of the period in the treatment that was then producing close to the maximum growth rate for the site (168 kg $ha^{-1}\ year^{-1}$ N). Although

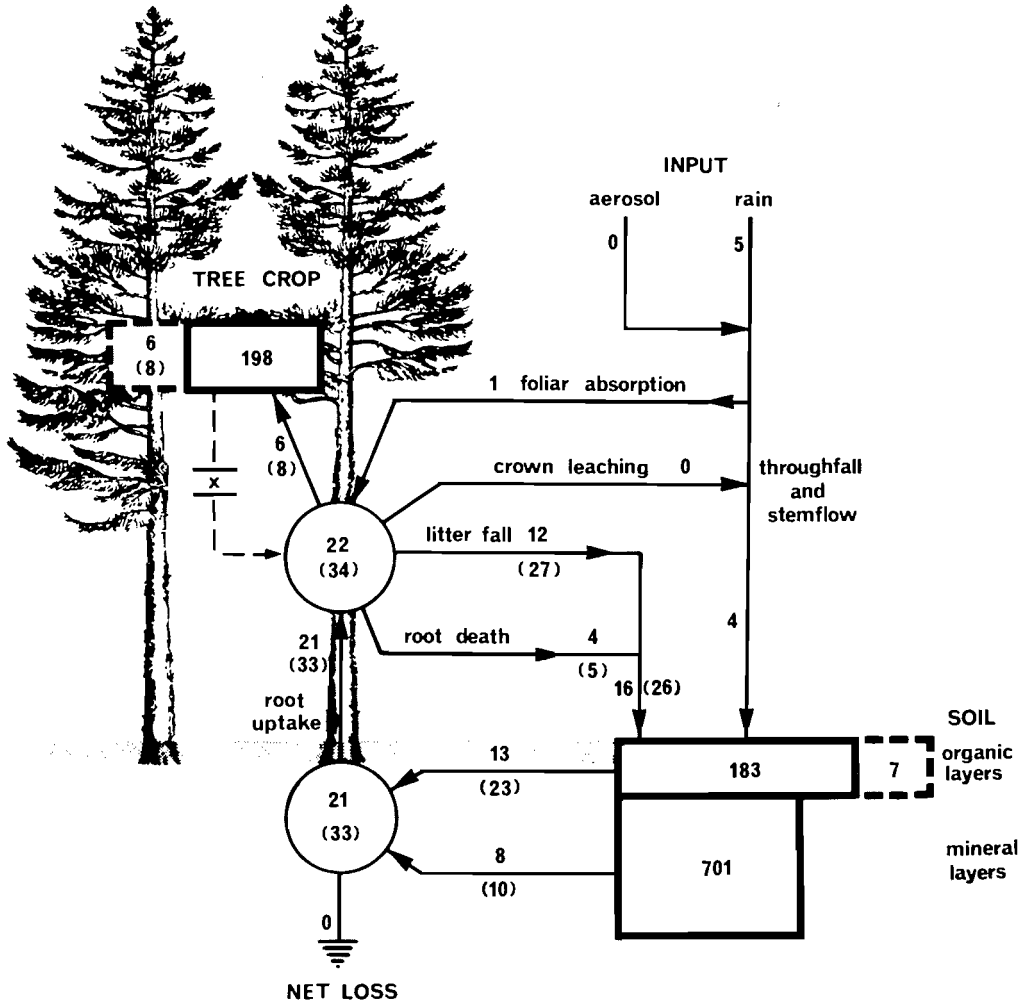

FIG. 1. Annual nitrogen budget in unfertilized trees. Nitrogen concentration in top-whorl foliage was 0.88%, basal area growth was 0.75 $m^2\ ha^{-1}\ year^{-1}$, and volume growth was 7.2 $m^3\ ha^{-1}\ year^{-1}$. Zones of accumulation are shown by rectangles, the annual rate of new accumulation being represented by the dashed portion. Mobile pools are depicted by circles. Link x between accumulation and mobile pool in the tree represents potential mobilization from second-level sources (see text). Values for accumulation are expressed in kilograms per hectare (kg ha^{-1}) and rates of accumulation and fluxes are in kilograms per hectare per year (kg $ha^{-1}\ year^{-1}$). Growth of these trees was declining progressively; the fluxes estimated from the model as being necessary to sustain a steady growth rate are shown in parentheses.

rates of accumulation in the root system were known, no means were found for obtaining realistic measures of the rate of nutrient release by root death and exudation. Allowance for this flux, therefore, was made by assuming that the ratio of release to the total weight accumulated is similar in both the root and shoot systems (Andersson 1970; Whittaker and Woodwell 1971).

Nutrient Cycles

The concept of nutrient cycling used here is illustrated in Fig. 1. As with any ecosystem, there is an input of nutrients from the atmosphere both in rain and *via* a further pathway, not adequately sampled by normal rain gauges, that it is convenient to term aerosol input (although it certainly includes other inputs in addition to that in true aerosols). This aerosol input, together with the elements derived from crown leaching, is washed from the tree surfaces by rain. A method was developed to estimate the separate contributions from these two sources (Miller, Cooper, and Miller 1976). However, this method measures as crown leaching the resultant between true crown leaching and foliar absorption, and in the figures, therefore, these processes appear to be mutually exclusive.

The soil receives nutrients in throughfall and stemflow, in litter fall, and through root death. As root death provides a source of fresh organic matter, it can be regarded as a contribution to the soil organic layers (although only 25% of the weight of lateral roots were actually located in these horizons). Since a certain portion of each nutrient reaching the soil organic layers becomes immobilized in the microbial biomass, or fails to mineralize, nutrients progressively accumulate on the forest floor at a rate broadly proportional to the rate of receipt in dead organic matter, which, in turn, is a function of growth rate (Miller and Miller 1976). The difference between receipt and accumulation forms part of the mobile pool of that element in the soil, a pool that has to supply both the uptake by the trees and other losses sustained by the soil, such as through leaching or denitrification. Any shortfall between these demands on the pool and the contribution of mobile nutrients through the soil organic layers has then to be made up by a fresh input to the cycle from the mineral soil horizons.

The concept of a pool of mobile nutrients in the soil is well understood. Recently, Fagerström and Lohm (1977) have emphasized the advantages of thinking in terms of mobile (or potentially mobile) and nonmobile (structurally bound) forms of nutrient within the tree, the concentration of the mobile form of a deficient element being the primary determinant of growth rate. It would seem useful to develop this further by suggesting two levels of mobility. The first level is represented simply by recent root and foliar uptake and includes temporary seasonal storage. Under equilibrium conditions, these would be the only sources of mobile nutrients tapped by the tree. The second level is represented by potentially mobile forms that can be used to make up, at least in part, for an inadequate supply from first-level sources. This can be by mobilization of reserves previously accumulated in excess of the then requirements for growth, as can happen during heavy fertilizer application (Miller, Miller, and Pauline 1976). However, more usually, such mobilization occurs at a suboptimum level of nutrition and is at the expense of the proper functioning, or even continued existence, of older tree tissues, a sacrifice that is inevitably accompanied by a reduction in growth. Mobilization of accumulated reserves might be expected to maintain maximum growth until the stored excess is exhausted. In practice, however, the tree seems to husband this supply, and growth declines progressively, there being no discontinuity to mark the change from dependence on reserves to an active sacrifice of older tissues.

In the figures, the pool of mobile nutrients at the first level is depicted as being analogous to the pool of mobile nutrients in the soil. This mobile pool is linked to the accumulated weight within the tree crop by a loop through which nutrients mobilized from second-level sources can be drawn if required. The size of any flux through this loop will depend on demand and availability, availability increasing with the weight of the crop and decreasing exponentially as the mean nutrient concentration in the tree declines.

The amount of nutrient within the mobile pool has to cover increased accumulation of nutrients in new tree tissues and the net release through root death, litter fall, and recruitment to the standing crop of dead branches (i.e., the release after retranslocation of a portion of the nutrient back into the surviving tissues of the plant). The rate of release through branch death was calculated for each nutrient. The values, however, are small and in the figures have been added in with those for release through litter fall.

Nitrogen Stress and Response to Fertilizer

Addition of nitrogen in aerosols (Fig. 1) is insignificant, but rainwater provides a useful source from which there may even be direct foliar uptake if trees are very deficient. In the unfertilized plots, roughly equal quantities of nitrogen had accumulated in the living trees and soil organic layers and together these accounted for over a third of the very low nitrogen capital of the site. Immobilization in the still developing soil organic layers was continuing to remove 7 kg ha^{-1} nitrogen from the cycle per year, leaving only enough mobile nitrogen to satisfy two thirds of the trees's requirements. The remaining 8 kg has then to come from the capital of some 700 kg ha^{-1} nitrogen in the mineral horizon. As there was no loss of nitrogen from the site, it appears that 8 kg ha^{-1} $year^{-1}$ is a real measure of the nitrogen-supplying ability of these mineral horizons.

The models of nitrogen fluxes suggest that to maintain the current growth rate of the unfertilized trees, the nitrogen supply from the mineral soil would have to be slightly increased, the loss by accumulation in tree tissues would rise by a third, and movement in litter fall would be much increased. The difference between rates of accumulation is interesting as it indicates that in reality the trees were having to mobilize about 2 kg ha^{-1} $year^{-1}$ nitrogen from second-level sources *via* loop x. Certainly nitrogen concentration within the tree tissues decreased over the 3 years between samplings, and there has been a continuing decline in the growth of these trees

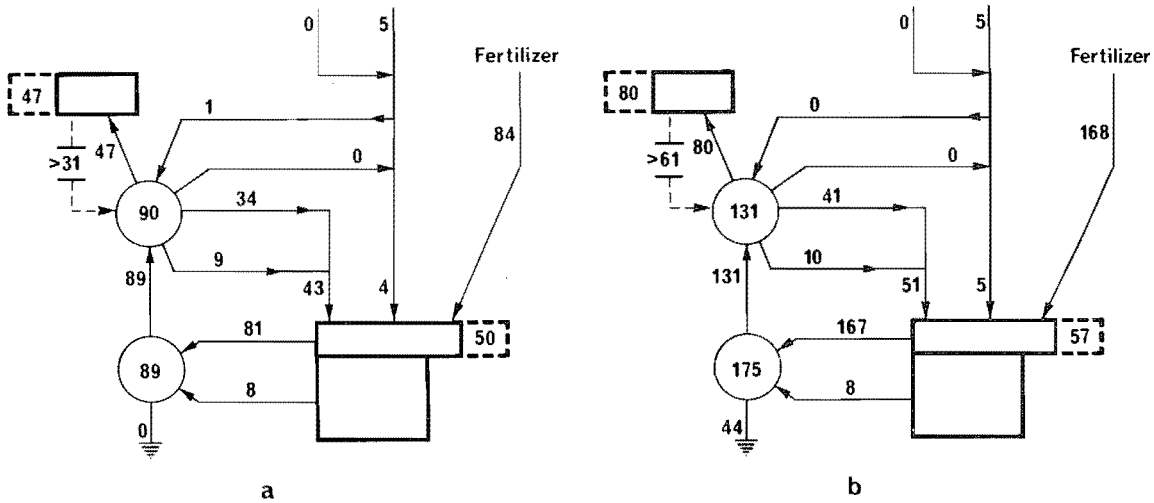

FIG. 2. Measured annual nitrogen budgets at two rates of fertilizer input, both applied over 3 years. By the last year of this period, input of 84 kg N (*a*) had produced a nitrogen level in top-whorl foliage of 1.55%, a basal area growth of 1.71 m^2 ha^{-1} $year^{-1}$, and a volume growth of 16.7 m^3 ha^{-1} $year^{-1}$. Input of 168 kg N (*b*) produced a nitrogen level of 2.01%, at which level growth was maximum for the site, being 2.09 m^2 ha^{-1} $year^{-1}$ basal area and 19.7 m^3 ha^{-1} $year^{-1}$ volume. For explanation of symbols see Fig. 1.

(Miller, Miller, and Pauline 1976). The large difference between measured and estimated values for movement in litter fall is partly because the estimated values are based on 6, rather than 3, years data, annual litter fall being a very variable parameter.

The measured flux in two fertilizer treatments is illustrated in Fig. 2. At the lower treatment rate, all the nitrogen applied, 252 kg over 3 years, was retained, approximately equal amounts being accumulated in the trees and in the soil organic layer. At the higher rate of application, however, a loss of 44 kg occurred, this being about a quarter of the fertilizer input. As fertilizer rates increased, so did the losses, rising to 55% at a rate of 504 kg ha^{-1} $year^{-1}$ fertilizer nitrogen (Miller, Miller, and Pauline 1976). Nevertheless, the amount of fertilizer nitrogen than can be recovered illustrates how effectively nitrogen is retained in such ecosystems.

A measure of the amount of the nitrogen newly accumulated within the tree that could subsequently be remobilized from second-level sources was calculated by allowing the nitrogen concentrations and weights of ephemeral tree components in fertilized trees to decline to pretreatment levels. On an annual basis, this amounted to 31 and 61 kg ha^{-1} nitrogen in the two treatments shown in Fig. 2 and was as high as 113 kg in the heavy, 504 kg, treatment. Thus, rather more than two thirds of the nitrogen taken up during fertilizer application is available for growth in subsequent years. Indeed, Miller, Miller, and Pauline (1976) have calculated that all the enhanced growth shown by these nitrogen-fertilized trees in the years after cessation of fertilizer application can be explained in terms of remobilization from second-level sources.

Nutrient Cycles at Optimum Growth

Maximum growth on this site, 2.09 m^2 basal area and 19.7 m^3 volume ha^{-1} $year^{-1}$, occurs at a nitrogen level in top-whorl foliage of 2.01% (Miller and Cooper 1973), the associated levels of other major nutrients being 0.16% phosphorus, 0.83% potassium, 0.18% calcium, and 0.09% magnesium. The fluxes of each element required to maintain this rate of growth are shown in Figs. 3 to 7. In these, the contribution from the mineral soil horizons is a minimum value as it would also have to cover any losses from the site.

For phosphorus like nitrogen, there is no significant input in aerosols, but for potassium, calcium, and magnesium, this is an important source. In addition, crown leaching contributes large amounts of potassium and magnesium to the rainwater passing over the trees.

Examination of the variation between plots in the weights of nutrients accumulated in the soil organic layers before treatment suggested that at least up to this stage in the rotation, the rate of accumulation was a simple function of basal area increment. The pretreatment rates of accumulation, therefore, have been increased by the ratio of maximum basal area increment to pretreatment mean values ($\times$ 1.37) to give the rates of accumulation shown in the figures. The significance of accumulation in the soil organic

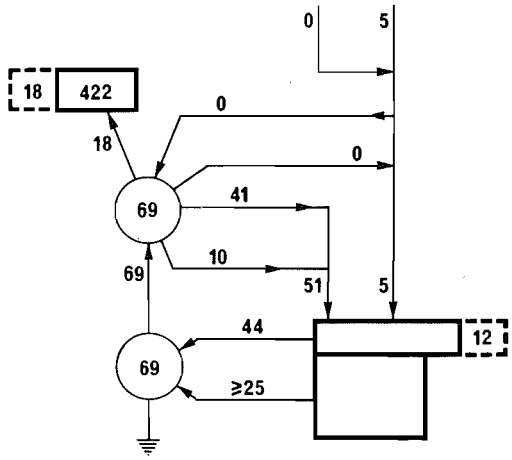

FIG. 3. Calculated annual fluxes and rates of accumulation of nitrogen required to maintain maximum growth (19.7 m^3 ha^{-1} $year^{-1}$). For explanation of symbols see Fig. 1.

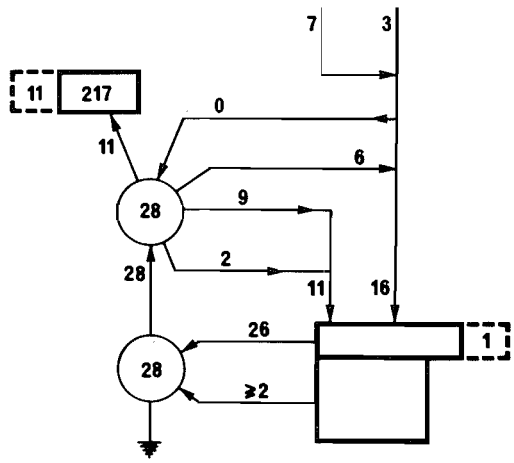

FIG. 5. Calculated annual fluxes and rates of accumulation of potassium at maximum growth rate. For explanation of symbols see Fig. 1.

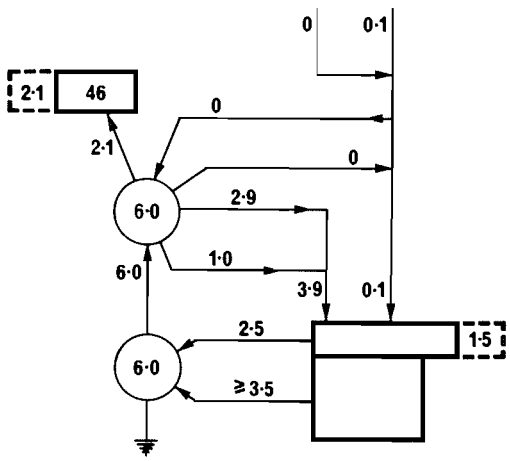

FIG. 4. Calculated annual fluxes and rates of accumulation of phosphorus at maximum growth rate. For explanation of symbols see Fig. 1.

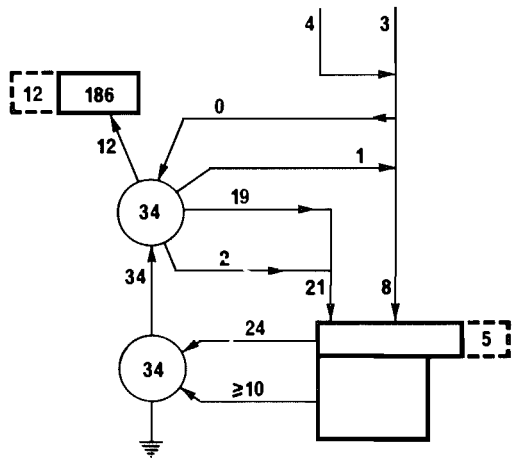

FIG. 6. Calculated annual fluxes and rates of accumulation of calcium at maximum growth rate. For explanation of symbols see Fig. 1.

layers varies between the five nutrient elements. At one extreme is phosphorus, for which 1.5 kg or 38% of the input to the soil organic layers remains to accumulate. Next come nitrogen and calcium, at 21% and 17%, respectively, while for magnesium and potassium, the proportions are only 13% and 4%. The corollary is that whereas the trees have to obtain 58% of their phosphorus requirements from the mineral soil horizons, these contribute only 36% of the nitrogen and 29% of the calcium uptake and as little as 6% and 7% of the magnesium and potassium uptake.

The extent to which trees can become independent of the mineral soil as a source of potassium and magnesium is quite striking. Deficiencies of these elements are not very common (Leaf 1968). Notable exceptions are plantations on degraded soils with a very low capital of either element, such as the potassium deficiencies recorded on sandy outwash soils in New York State (Heiberg and White 1950) and on peat bogs in Britain and Ireland (Binns 1962; O'Carroll 1966). In the former area, *Pinus resinosa* Ait. has shown responses lasting more than 25 years to a single application of potassium fertilizer. Stone and Kszystniak (1977) have recently demonstrated that this persistence is due to a high retention of the added potassium within the cycle, an explanation that accords well with the model fluxes shown in Fig. 5.

Thus, the annual loss from the cycles of potas-

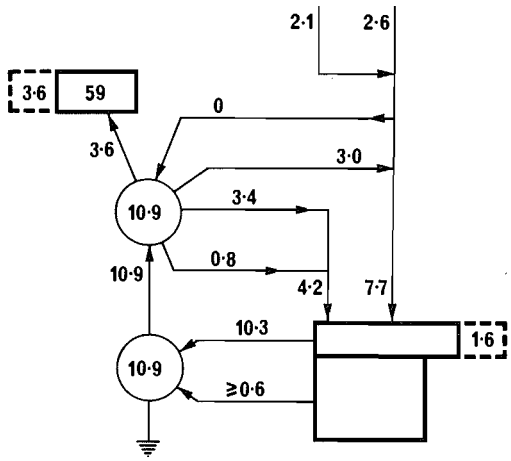

FIG. 7. Calculated annual fluxes and rates of accumulation of magnesium at maximum growth rate. For explanation of symbols see Fig. 1.

sium and magnesium through immobilization is small relative to the amount being cycled, and this loss can, to a very large extent, be replaced by the input in rain and aerosols. Although the input will be lower in more inland regions (Robertson and Davies 1965; O'Carroll and McCarthy 1973), it seems unlikely that coniferous trees would ever have to make large demands on the mineral soil for either of these elements once the cycles have become established. For the other three nutrients, however, even when a tight cycle has become established, i.e., there were no losses of nitrogen (Figs. 1 and 2) and phosphorus does not leach, the trees make continuing demands on the mineral soil layers to replace high rates of accumulation. As deficiencies of calcium are virtually unknown, it seems that trees have no difficulty in obtaining adequate supplies of this element from all soil types. In the case of nitrogen and phosphorus, on the other hand, deficiencies are not uncommon, particularly in northern regions (Tamm 1968). For these elements, not only does a large proportion of the available capital become immobilized in dead organic matter, but also the inputs from the atmosphere are low relative to the demands of the crop. Loss through immobilization, therefore, has to be compensated for by fresh supplies from the lower soil horizons. For nitrogen, in particular, the rate of immobilization may be such that previously healthy trees become progressively deficient as an unacceptable proportion of the limited nitrogen capital becomes immobilized in the organic layers (e.g., Tamm *et al.* 1960; Weetman 1962; Heilman 1966; Miller and Cooper 1973).

In conclusion, it seems that tight cycling and low rates of immobilization of the limited supplies of potassium and magnesium, together with the effective retention of atmospheric inputs, may represent the adaptive mechanism that enables coniferous trees to thrive on soils low in these nutrients. However, high rates of immobilization and low atmospheric inputs mean that this mechanism is not sufficient to guarantee supplies of nitrogen and phosphorus. This is despite the fact that the cycle of both these elements is tight, losses beyond the rooting zone being negligible, and that, at least for nitrogen, all the atmospheric input is retained. For these elements, then, the trees have to rely on obtaining nutrients from intractable soil sources, and here, presumably, the mechanism has been the evolution of the mycorrhizal relationship, a relationship that confers a particular advantage in obtaining nitrogen and phosphorus from poor soils (Harley 1969). Indeed, the fact that mycorrhizal fungi appear to be most efficient at obtaining phosphorus for the host plant may explain why deficiencies of this element in established forests are reported less frequently than are deficiencies of nitrogen.

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